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Role of Glandular Trichomes and Terpene Diversity on Tomato Resistance against the Sweetpotato Whitefly

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Abstract. **Sweetpotato whiteflies, *Bemisia tabaci* Genn. (Hemiptera: Aleyrodidae), are major agricultural pests that may significantly reduce tomato yields, particularly in *Solanum lycopersicum* cultivars with limited natural resistance. This study investigates whitefly host plant resistance mechanisms in accessions of wild tomato species that have high glandular trichome densities and distinctive sesquiterpene production. Through a field experiment with a complete randomized block design, we evaluated a natural *B. tabaci* population dynamic, leaf trichome density, and terpene profiles across selected wild accessions of *Solanum habrochaites* (G29258, PI126449, PI127826, PI134418, PI209978), *Solanum galapagense* (LA1401), and *Solanum chilense* (LA1932), as well as cultivars of *S. lycopersicum* (LA3475, Cherry Bomb, Apple Yellow, Patsy, and Mountain Man). These wild accessions exhibited significantly lower whitefly densities of nymphs that were closely associated with high glandular trichome presence and increased levels of the sesquiterpenes, including terpinolene, α-zingiberene, 9-hydroxy-10,11-epoxy-zingiberene, and 9-hydroxy-zingiberene, which are known for their natural repellent properties. Multivariate analyses revealed an apparent clustering of terpene-rich wild accessions with enhanced whitefly resistance. These results emphasize the critical role of glandular trichomes and their secreted terpenes in natural pest resistance, distinguishing wild accessions from cultivars. This study highlights the breeding potential of wild tomato accessions for developing pest-resistant cultivars and advancing sustainable pest management in tomato cultivation.**

The sweetpotato whitefly, *Bemisia tabaci* Genn. (Hemiptera: Aleyrodidae), is a major global agricultural pest, impacting vegetable crop production due to direct damage to plants by feeding on their sap and indirect damage by transmitting plant viruses (Andreason et al. 2020; Navas-Castillo et al. 2011). In tomato, infestations can result in yield losses of up to 100% in highly susceptible cultivars and cause tens of millions of dollars in economic losses (Fonsah et al. 2018). Managing whitefly populations is particularly challenging due to the rapid emergence of pesticide resistance and the ecological impacts and human health risks associated with pesticide overuse (Cremonez et al. 2023; Desneux et al. 2007; Horowitz et al. 2020; Rutz et al. 2023). Widespread insecticide use has disrupted natural enemy and pollinator communities, contributed to biodiversity loss, and led to the evolution of resistant *B. tabaci* populations (Horowitz et al. 2020). In the United States, more than 120 resistance cases involving 17 different a.i. have been reported in *B. tabaci* populations (Mota-Sanchez and Wise 2025). In addition, persistent residues of pesticides such as malathion and chlorpyrifos, both associated with *B. tabaci* resistance, are frequently detected in surface waters in the United States, raising further concern for environmental and public health (Mota-Sanchez and Wise 2025; Sharma et al. 2019). Chronic pesticide exposure also poses significant health risks to farm workers and surrounding communities, including respiratory illnesses, endocrine disruption, and other long-term effects (Damalas and Eleftherohorinos 2011; Zhou et al. 2025). These concerns underscore the need for improved integrated pest management (IPM) strategies that reduce chemical dependency while maintaining crop productivity.

One sustainable strategy gaining attention involves harnessing plant-based defense mechanisms, particularly those driven by specialized metabolites (Andrade et al. 2017; Divekar et al. 2022; Souto et al. 2021). Among these, terpenes, ranging from simple monoterpenes to complex sesquiterpenes and sesterterpenes, are known to interfere with insect feeding and physiology, serving as natural deterrents (Divekar et al. 2022; Mabou and Yossa 2021; Tilkat et al. 2023). Their defensive roles and metabolic diversity make them attractive targets for breeding pest-resistant cultivars through conventional or molecular approaches (Souto et al. 2021).

Wild tomato species from *Solanum* section *Lycopersicon* possess strong natural resistance to a range of insect pests (Kortbeek et al. 2021; Rutz et al. 2024). Compared with cultivated *S. lycopersicum*, wild species such as *S. habrochaites* (Bennewitz et al. 2018; Bergau et al. 2015; Therezan et al. 2021) and *S. galapagense* (Henzler and Khazaei 2024; Vendemiatti et al. 2021, 2022) produce high densities of glandular trichome (particularly types IV and VI) that secrete defensive compounds including acylsugars and terpenes (Bleeker et al. 2009a, 2009b; Dawood and Snyder 2020; Fürstenberg-Hägg et al. 2013; Schilmiller et al. 2008). For example, *Solanum pennellii* Correll is known for its production of acylsugars (Resende et al. 2006), while *S. habrochaites* S. Knapp & D.M. Spooner var. *hirsutum* synthesizes zingiberene, a sesquiterpene associated with whitefly resistance (Bleeker et al. 2011; Dawood and Snyder, 2020; Maluf et al. 2001). Several studies have demonstrated that these trichome-derived compounds significantly reduce *B. tabaci* survival and oviposition (Almeida et al. 2023; Rakha et al. 2017; Silva et al. 2014; Zeist et al. 2021).

These resistance traits have been successfully introgressed into cultivated tomato lines via interspecific hybridization, resulting in genotypes with elevated levels of insect-deterring compounds (Neiva et al. 2019). Importantly, such wild-derived traits are compatible with biological control agents and other IPM tools, supporting synergistic pest suppression in the field (Andrade et al. 2017; Neiva et al. 2019; Vosman et al. 2018). Their use reduces pesticide use, protects beneficial organisms, lowers production costs, and minimizes residue levels on produce, delivering clear environmental and economic benefits to both farmers and consumers (Rakha et al. 2017).

In this context, profiling terpene composition and trichome morphology in wild tomato accessions provides valuable insights for identifying and using resistance traits in breeding programs (Wang et al. 2020). A deeper understanding of this phytochemical diversity enables precision breeding and metabolic engineering strategies to improve pest resistance in cultivated tomatoes. Continued exploration of wild tomato relatives offers promising pathways toward developing durable, pest-resistant varieties aligned with sustainable agriculture practices (Kashyap et al. 2022).

This study aimed to investigate whitefly resistance in selected wild tomato accessions of *S. habrochaites*, *S. galapagense*, and *S. chilense*, as well as cultivars of *S. lycopersicum*, with a focus on characterizing both glandular and nonglandular trichomes, identifying and quantifying terpenes, and correlating these factors with reductions in whitefly populations.

Materials and Methods

Experimental design and field management. A study using a randomized complete block design with three blocks, each representing a replication, was conducted at the Wiregrass Research and Extension Center, Auburn University, Headland, AL, USA (31°21′26″N, 85°19′24″W), to evaluate the effects of different wild tomato accessions on *B. tabaci* populations. The treatments included seven wild tomato accessions (detailed in Supplemental Table 1) and five tomato cultivars as controls. Five wild accessions—G29258, PI127826, PI134418, PI209978, and PI126449—from *S. habrochaites* were sourced from the US Department of Agriculture-Agricultural Research Service Germplasm Resources Information Network-Global. The wild accessions LA1401 (*S. galapagense*), LA1932 (*S. chilense*), and the cultivar LA3475 (*S. lycopersicum* 'M-82') were obtained from the C.M. Rick Tomato Genetics Resource Center, University of California, Davis, CA, USA. Four *S. lycopersicum* cultivars were also included: the beefsteak tomatoes Patsy (Bejo Seeds, Oceano, CA, USA) and Mountain Man (Syngenta US, Greensboro, NC, USA), and the cherry type of tomatoes Cherry Bomb and Apple Yellow (Johnny Seeds, Waterville, ME, USA). Each experimental unit was a single row with five plants, with data collected from the central three plants to reduce edge effects.

Tomato seeds for wild accessions and cultivars were sanitized in a 10% sodium hypochlorite solution for 5 minutes before sowing. On 21 Jul 2023, seeds were planted into 36 mm peat pellets (Jiffy Group, Lorain, OH, USA) and placed in 28 °C growth chambers for germination. Seedlings were transplanted into the field on 23 Aug 2023. The field, with sandy soil, featured 15-cm-tall raised beds spaced 1.8 m apart, with 30 cm between plants. Uniform cultural practices, including irrigation, fertilization, pest, disease, and weed management, were applied according to the Southeastern US 2022 Vegetable Crop Handbook (Kemble et al. 2022).

Data collection. Whitefly populations were monitored weekly, starting 30 d after transplanting (DAT), when the first adult whiteflies were observed. Counts were conducted at 30, 37, 44, 51, and 58 DAT by visually inspecting the underside of two leaves from the lower third of three different plants per plot, sampled before 0900 HR to minimize the influence of temperature, sunlight, or insect movement. This sampling strategy resulted in a total of 90 leaves per genotype (n = 2 leaves × 3 plants × 3 plots × 5 DATs). In addition, counts of whitefly nymphs and eggs were conducted in the laboratory at 44, 51, and 58 DAT to evaluate the effect of the treatment on immature stages. On each date, one leaf per plant was collected from three plants per plot across three replicate plots, resulting in 27 leaves per genotype (n = 1 leaf × 3 plants × 3 plots × 3 DATs). Collected leaves were placed in a zip sealed bag and examined under a Leica® M165 C Stereo Microscope (Leica Microsystems, Wetzlar, Germany) with a ×5 to ×20 magnification. A 1-cm^2 area from each leaflet's terminal part was randomly selected, and the numbers of whitefly nymphs and eggs on the abaxial surface of that area were recorded for statistical analysis.

Environmental data (rainfall and daily air temperature) were recorded using an on-site Vantage® Pro2 Plus (Davis Instruments, Hayward, CA, USA) weather station to contextualize fluctuations in whitefly populations and assess the impact of environmental factors on plant performance and whitefly infestations across treatments (Supplemental Table 2).

Tomato leaf trichome characterization. At 62 DAT, one fully developed young leaf from the upper third of each plant at the preflowering stage was collected from three plants per plot across three replicate plots, resulting in nine leaves per genotype (n = 1 leaf × 3 plants × 3 plots × 1 DAT) for trichome identification and quantification. The leaflets were placed in zip seal bags and transported to the laboratory, where they were stored at room temperature (25 °C) until scanning electron microscope (SEM) analysis was conducted the following day. For SEM preparation, three small paradermal fragments ($10\ \text{mm}^2$ each) from the upper, middle, and lower abaxial surfaces of the leaflets were mounted on aluminum stubs with carbon tape and coated with gold using a sputter-coating machine (EMS Q150R SCD, Quorum Technologies, Calgary, AB, Canada). Photomicrographs were captured with an SEM (EVO 50; Carl Zeiss Vision Inc., Hebron, KY, USA) at ×500 magnification and 20 kV voltage. Trichomes on the abaxial leaflet surface were counted and classified as glandular or nonglandular according to established methodology (Channarayappa et al. 1992; Toscano et al. 2001).

Reagent, solvent, and terpene extraction. Certified terpene mixture ($2500\ \mu\text{g}\cdot\text{mL}^{-1}$ in isopropanol of eucalyptol, (−)-α-bisabolol, camphene, δ-3-carene, β-caryophyllene, geraniol, (−)-guaiol, α-humulene, p-cymene, isopulegol, D-limonene, linalool, β-myrcene, nerolidol, β-ocimene, α-pinene, (−)-β-pinene, α-terpinene, γ-terpinene, terpinolene, and (−)-caryophyllene oxide) were purchased from Restek Corp (Bellefonte, PA, USA). α-zingiberene (≥95%) was obtained from Alfa-chemistry (Ronkonkoma, NY, USA).

A stock standard solution ($125\ \mu\text{g}\cdot\text{mL}^{-1}$) of terpenes was prepared by appropriately diluting the original standard in hexane and stored at −18 °C. Working standard solutions at different concentration levels were prepared by appropriately diluting the stock solutions in n-hexane (VWR International LLC, Radnor, PA, USA) and stored at −18 °C.

Terpenes were extracted from intact tomato leaflet trichomes using a standardized leaf dip method (Pizzo et al. 2024). For each genotype, leaves were collected from plants grown in separate replicate plots. From each plant, 0.1 to 0.5 g of tomato leaflets were placed in centrifuge tubes with 5.0 mL of n-hexane. The mixture was shaken for 2 min at 25 ± 2 °C. After extraction, the solution was centrifuged at $9000\ g_n$ for 2 min, and the supernatant was transferred into gas chromatography–mass spectrometry (GC-MS) glass vials.

GC-MS analysis. GC-MS analysis was performed using an Agilent 5977B GC/MSD (Agilent Technologies, Santa Clara, CA, USA) following established methodology (Pizzo et al. 2024). Terpenes were separated on an HP-5MS column (30-m × 250-μm-diameter capillary, 0.25-μm film thickness). A 1.0 μL injection was made in splitless mode at 300 °C, with a solvent delay of 4 min. The temperature program for the GC oven was as follows: 50 °C for 1 min, then increased to 300 °C at a rate of 7 °C/min, followed by an increase to 320 °C at 20 °C/min, where it was held for 2 min. Helium was used as a carrier gas at a constant flow rate of $1\ \text{mL}\cdot\text{min}^{-1}$, and terpenes were ionized using electron ionization at 70 eV. The transfer line and ion source

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temperatures were maintained at 250 and 230 °C, respectively. MS data were acquired in scan mode over 50 to 550 *m/z*. All samples and standards were injected into triplicate. To prevent contamination, a hexane blank was included after every three sample runs.

Terpenes were identified through retention time (RT) matching and mass spectral library searches, including the National Institute of Standards and Technology (NIST) MS spectral database (version 2.4, 2020). Authentic standards were used to confirm the identity of specific compounds when available. In cases in which standards were unavailable, identification was based on achieving an NIST library matching score greater than 80%. Compounds were categorized as "similar to" the matched compound scores between 80% and 90% and definitively identified for scores between 91% and 100%. Compounds with matching scores below 79% were classified as unidentified and excluded from the reported results. Identification was performed using MassHunter Qualitative Analysis software (version 10.0).

Quantitative analysis was performed using the external calibration curves created with a terpene standard mix. Calibration curves were constructed at seven concentrations ranging from 0.2 to 10 $\mu g \cdot mL^{-1}$. The method's linearity, limits of detection (LOD), and limits of quantification (LOQ) were evaluated. LOD values were calculated as 3.3 times the standard deviation (*SD*) divided by the slope (b) of the calibration curve and LOQ was determined as 10 × *SD*/b. Quantification was conducted with Agilent MassHunter Quantitative Analysis software (version 10.2). A qualifier ion was employed to identify each analyte, and a quantifier ion was used to determine the analyte response via peak calculation from the extracted ion chromatogram. Specific standards were used to semiquantify the leaf extract components for components not included in the terpene standard mix. D-limonene, 3-carene, and α-humulene from the terpene standard mix were used as external standards for monocyclic monoterpenes, bicyclic monoterpenes, and monocyclic sesquiterpenes, respectively. The terpene content was expressed as $\mu g \cdot g^{-1}$ fresh weight.

Statistical analysis. Repeated measures analysis was used to evaluate temporal changes in whitefly adults, nymphs, and eggs, modeling the variance-covariance structure with PROC-GLIMMIX in SAS (version 9.4, 2024) using restricted maximum likelihood. This approach accounted for correlations from repeated sampling, employing a heterogeneous compound symmetry structure for the variance-covariance matrix. The significance of correlations was assessed at $P \leq 0.05$ with Pearson's coefficient. Accessions were considered fixed effects and blocks were included as random effects. Orthogonal contrasts facilitated comparisons between wild accessions and cultivars. Nymph, egg, and trichome counts were analyzed under a Negative Binomial distribution with a logit link function using the Laplace approximation. Tukey's test was applied for post hoc mean comparisons with a significance threshold of $P \leq 0.05$.

Multivariate analysis included whitefly nymph counts, glandular and nonglandular trichome densities, and terpene content detected via GC-MS to identify associations between wild tomato accessions and tomato cultivars and test for correlation among measurements. Pearson's correlation matrix (Supplemental Table 3) significant correlations ($P \leq 0.05$ or $P \leq 0.01$) were submitted to correlation-based network analysis (CNA) to investigate and graphically represent the correlation among variables analyzed (Epskamp et al. 2012; Wei and Simko 2021). A heatmap displayed trait patterns, while Euclidean distance and unweighted pair group method with arithmetic hierarchical clustering produced dendrograms grouping accessions by variable similarity (Gu et al. 2016). Principal component analysis (PCA) was further used to evaluate relationships among whitefly nymphs, trichome densities, and terpene profiles based on their contributions to principal components (Kassambara 2017; Lê et al. 2008).

Results

Whitefly population and trichome density (nonglandular vs. glandular). There was no statistically significant interaction between repeated assessments of whitefly populations over time and tomato plant treatments ($P > 0.05$). However, a significant main effect of wild tomato accessions and tomato cultivars on whitefly populations was observed in the density of nymphs per cm^2 ($P \leq 0.05$) (Table 1). Although no significant differences were found for adults and egg densities, there were significantly fewer nymphs on the wild tomato accessions, including *S. habrochaites* (G29258, PI126449, PI127826, PI134418, PI209978), *S. galapagense* (LA1401), and *S. chilense* (LA1932) as compared with the cultivars of *S. lycopersicum* (LA3475, Cherry Bomb, Apple Yellow, Patsy, and Mountain Man) (Table 1). On average, the cultivars harbored 1.8 adults per leaf, 5.6 nymphs/cm^2, and 1.8 eggs/cm^2, whereas wild accessions harbored 1.4 adults per leaf, 0.3 nymphs/cm^2, and 0.7 eggs/cm^2 (Table 1 and Fig. 1A). Among cultivars, Apple Yellow and Cherry Bomb were the most susceptible, with infestation rates of eight and seven nymphs per cm^2, respectively.

Significant differences were also observed in trichome numbers and types across accessions and cultivars (Table 1). *S. lycopersicum* cultivars exhibited a higher density of nonglandular trichomes, averaging 55 nonglandular trichomes per μm^2, compared with an average of 20 nonglandular trichomes per μm^2 in wild accessions. Among the cultivars, Apple Yellow had the highest density, with 73 nonglandular trichomes per μm^2. Most wild accessions had lower densities of nonglandular trichomes, with LA1401, PI127826, and PI209978 completely lacking them. In contrast, glandular trichomes were present in wild accessions, averaging 15 glandular trichomes per μm^2, but were generally absent in *S. lycopersicum* cultivars. The wild accessions LA1401 (27 glandular trichomes per μm^2) and PI209978 (26 glandular trichomes per μm^2) had the highest densities of glandular trichomes. All *S. lycopersicum* cultivars (LA3475, Cherry Bomb, Apple Yellow, Patsy, and Mountain Man) had no glandular trichomes. Scanning electron micrographs of trichomes across different genotypes are shown in Fig. 1B.

Terpene profile and content in tomato plants. The external calibration curves for the 22 terpene standards demonstrated high linearity within the concentration range of 0.2 to 10 $\mu g \cdot mL^{-1}$, with r^2 values ranging from 0.9936 to 0.9994 (Table 2). This strong correlation between analyte concentration and detector response indicates that the method

Table 1. Mean numbers of *Bemisia tabaci* adults, nymphs, and eggs, and the distribution of nonglandular and glandular trichome densities from wild tomato accessions of *Solanum habrochaites* (G29258, PI126449, PI127826, PI134418, and PI209978), *Solanum galapagense* (LA1401), and *Solanum chilense* (LA1932), and cultivars of *Solanum lycopersicum* (LA3475, Cherry Bomb, Apple Yellow, Patsy, and Mountain Man).

	Mean number				
Genotype	Adults per leaf (n[i] = 90)	Eggs per cm^2 (n = 27)	Nymphs per cm^2 (n = 27)	Nonglandular trichomes per μm^2 (n = 9)	Glandular trichomes per μm^2 (n = 9)
Apple Yellow	2 ± 0	2 ± 1	8 ± 2 a[ii]	73 ± 6 a	0 ± 0 e
Cherry Bomb	2 ± 0	1 ± 1	7 ± 1 a	49 ± 4 b	0 ± 0 e
Mountain Man	2 ± 0	2 ± 1	4 ± 1 ab	53 ± 2 b	0 ± 0 e
Patsy	2 ± 0	1 ± 1	4 ± 2 ab	48 ± 2 b	0 ± 0 e
LA3475[iii]	1 ± 0	3 ± 1	5 ± 2 ab	51 ± 5 b	0 ± 0 e
LA1401	1 ± 0	1 ± 1	0 ± 0 b	0 ± 0 e	27 ± 2 a
LA1932	1 ± 0	2 ± 1	1 ± 0 b	48 ± 6 b	3 ± 1 de
G29258	2 ± 0	0 ± 0	0 ± 0 b	23 ± 3 d	6 ± 1 d
PI126449	1 ± 0	0 ± 0	0 ± 0 b	40 ± 3 bc	7 ± 1 d
PI127826	1 ± 0	0 ± 0	1 ± 1 b	0 ± 0 e	20 ± 2 b
PI134418	2 ± 1	0 ± 0	0 ± 0 b	30 ± 3 cd	14 ± 1 c
PI209978	2 ± 0	2 ± 1	0 ± 0 b	0 ± 0 e	26 ± 2 a
P value[iv]	ns	ns	*	*	*

[i] "n" means the number of leaves per genotype used to calculate the mean.

[ii] According to Tukey's mean test, values (mean ± standard error) followed by different letters indicate a significant difference ($P \leq 0.05$) among treatments.

[iii] *S. lycopersicum* 'M-82'.

[iv] Level of significance: "ns" is nonsignificant and "*" is significant at $P \leq 0.01$.

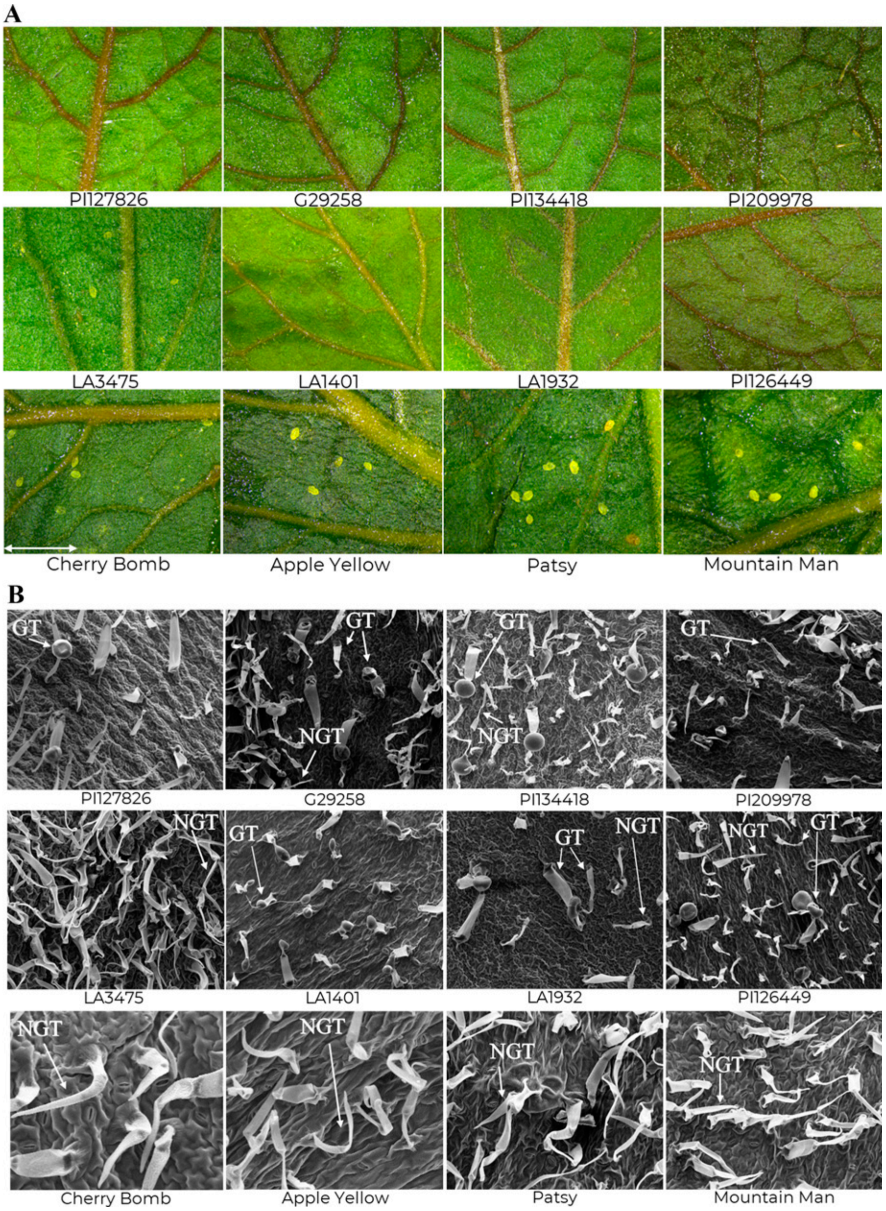

Fig. 1. (**A**) Microscope images of the abaxial surface of leaflets from tomato accessions and cultivars, and (**B**) scanning electron micrographs showing the abaxial surface of leaflets from wild tomato accessions of *Solanum habrochaites* (G29258, PI126449, PI127826, PI134418, PI209978), *Solanum galapagense* (LA1401), and *Solanum chilense* (LA1932), and cultivars of *Solanum lycopersicum* (LA3475, Cherry Bomb, Apple Yellow, Patsy, and Mountain Man). These images highlight the absence of *Bemisia tabaci* nymphs on the leaflets of most wild accessions and emphasize the morphological differences in trichome structures between wild tomato accessions and cultivars. Scale bars: 1 cm and 100 μm. GT = glandular trichomes; NGT = nonglandular trichomes.

can accurately quantify terpenes across a broad range of concentrations. The LOD for the various terpenes ranged from 0.02 to 0.30 $\mu g \cdot mL^{-1}$ and the LOQ varied between 0.2 and 0.9 $\mu g \cdot mL^{-1}$ (Table 2). These values demonstrate the method's sensitivity for detecting and quantifying terpenes in extracts from tomato leaflet trichomes. A hexane blank was randomly included in each run to assess potential carryover. No detectable analyte peaks were observed in the blank runs, indicating minimal carryover.

The field-grown wild tomato accessions and tomato cultivars were subjected to leaf dip extractions and were analyzed by GC-MS. The analysis identified 24 terpenes based on their RT and mass spectral patterns. Table 3 presents the identified compounds, including their RT, qualitative and quantitative ions (*m/z*), molecular formula, terpene content ($\mu g \cdot g^{-1}$), and classification. The classifications include acyclic monoterpenes, bicyclic monoterpenes, monocyclic monoterpenes, acyclic sesquiterpenes, monocyclic sesquiterpenes, and bicyclic sesquiterpenes. The variability of terpenes among wild accessions and cultivars highlighted substantial differences. Among the terpenes identified, α-pinene (<LOD – 15.99 $\mu g \cdot g^{-1}$), 4-carene (0.29–23.04 $\mu g \cdot g^{-1}$), α-phellandrene (<LOD – 3.46 $\mu g \cdot g^{-1}$), β-phellandrene (<LOD – 10.11 $\mu g \cdot g^{-1}$), β-caryophyllene (<LOQ – 23.51 $\mu g \cdot g^{-1}$), δ-elemene (<LOQ – 2.41), humulene (<LOQ – 7.81 $\mu g \cdot g^{-1}$), and α-zingiberene (1.27–27.77 $\mu g \cdot g^{-1}$) are common. However, their concentrations varied significantly across tomato accessions and cultivars.

PI209978 and PI127826 exhibited notably high concentrations of zingiberene-related sesquiterpenes, including 9-hydroxy-10,11-epoxy-zingiberene (28.93 $\mu g \cdot g^{-1}$ and 46.82 $\mu g \cdot g^{-1}$, respectively) and 9-hydroxy-zingiberene (30.19 $\mu g \cdot g^{-1}$ and 24.06 $\mu g \cdot g^{-1}$, respectively), which were absent in other tomato plants. Similarly, α-zingiberene was abundant in PI209978 and PI127826, with 27.77 $\mu g \cdot g^{-1}$ and 27.07 $\mu g \cdot g^{-1}$, respectively. In contrast, it was present at lower levels in other wild tomato accessions, including G29258 (2.96 $\mu g \cdot g^{-1}$), LA1401 (2.89 $\mu g \cdot g^{-1}$), LA1932 (1.44 $\mu g \cdot g^{-1}$), and in the cultivar Mountain Man (1.27 $\mu g \cdot g^{-1}$).

Multivariate analysis. Pearson's correlation matrix (Supplemental Table 3) highlighted key relationships among tomato plant traits, particularly the interplay between terpene content, trichome types, and pest resistance indicators, such as nymph density per cm^2. The CNA established significant correlations among terpenes associated with resistance traits (Fig. 2A). In this network, positively correlated compounds exhibited strong associations, particularly among 9-hydroxy-10,11-epoxy-zingiberene, 9-hydroxy-zingiberene, and α-zingiberene, as well as terpinolene, 9-hydroxy-zingiberene, and α-zingiberene. In addition, a significant correlation was observed between the number of nymphs per cm^2 and the number of nonglandular trichomes per μm^2. Conversely, negative correlations linked specific terpenes to nonglandular trichomes, highlighting an inverse relationship: tomato plants with higher concentrations of certain terpenes generally had fewer nonglandular trichomes and more glandular trichomes. Also, the number of glandular trichomes negatively correlates with the number of whitefly nymphs and nonglandular trichomes per μm^2.

The cluster analysis and heatmap (Fig. 2B) categorized wild tomato accessions and tomato cultivars based on terpene content, revealing distinct clustering patterns that highlight biochemical diversity. Wild accessions PI209978 and PI127826 formed a unique cluster characterized by higher levels of specific terpenes and a greater density of glandular trichomes, as well as a reduced number of nonglandular trichomes and lower nymph density—traits associated with enhanced pest resistance.

The PCA biplot (Fig. 2C) revealed two primary clusters, with principal components 1 (PC1, 71.2%) and 2 (PC2, 16.9%) explaining 88.1% of the total variance. Cluster 1, which includes PI209978 and PI127826, showed a high concentration of specific terpenes (9-hydroxy-10,11-epoxy-zingiberene, 9-hydroxy-zingiberene, and terpinolene) and a strong association with glandular over nonglandular trichomes. In contrast, cluster 2, which consists of the remaining wild accessions and all cultivars, had lower terpene concentrations, indicating that the wild

Table 2. Linear range, analytical curve equation, coefficient of determination (r^2), limit of detection (LOD), and limit of quantification (LOQ) of terpenes using gas chromatography–mass spectrometry analysis.

Compound	m/z	Linear range ($\mu g \cdot mL^{-1}$)	Equation[i]	r^2	LOD	LOQ
					($\mu g \cdot mL^{-1}$)	
α-pinene	136.13	0.2–10	y = 444197.97x − 5770.52	0.9994	0.04	0.20
camphene	136.13	0.2–10	y = 58906.73x − 6150.07	0.9973	0.02	0.20
β-pinene	136.13	0.2–10	y = 466560.03x − 33510.13	0.9994	0.08	0.20
β-myrcene	136.13	0.8–10	y = 268988.61x + 20149.47	0.9945	0.30	0.80
3-carene	136.13	0.2–10	y = 80430.35x − 8495.88	0.9973	0.03	0.20
α-terpinene	136.13	0.3–10	y = 406526.62x − 14314.80	0.9991	0.08	0.30
p-cymene	134.11	0.2–10	y = 1008313.29x + 327727.73	0.9985	0.03	0.20
d-limonene	136.13	0.2–10	y = 315219.90x − 7767.59	0.9988	0.06	0.20
eucalyptol	154.14	0.4–10	y = 79675.49x + 1919.79	0.9974	0.10	0.40
β-ocimene	136.13	0.2–10	y = 19761.08x − 1463.91	0.9982	0.06	0.20
γ-terpinene	136.13	0.6–10	y = 342875.25x + 35305.80	0.9936	0.20	0.60
terpinolene	136.13	0.2–10	y = 266143.69x − 21650.75	0.9985	0.07	0.20
linalool	154.14	0.9–10	y = 168475.87x − 18808.94	0.9979	0.30	0.90
isopulegol	154.14	0.3–10	y = 14947.22x − 4364.33	0.9968	0.09	0.30
geraniol	154.14	0.4–10	y = 39554.53x − 18295.90	0.9937	0.10	0.40
β-caryophyllene	204.19	0.2–10	y = 149241.79x − 14478.84	0.9993	0.07	0.20
humulene	204.19	0.2–10	y = 439459.88x − 47020.59	0.9993	0.06	0.20
α-zingiberene	204.19	0.2–10	y = 96782.78x − 26039.41	0.9969	0.06	0.20
nerolidol	222.20	0.3–10	y = 96964.72x − 40147.24	0.9954	0.09	0.30
caryophyllene oxide	219.17	0.2–10	y = 35558.48x − 5201.49	0.9988	0.05	0.20
guaiol	222.20	0.3–10	y = 18640.30x − 5078.66	0.9978	0.10	0.30
α-bisabolol	222.20	0.2–10	y = 170420.91x − 49991.29	0.9983	0.06	0.20

[i] y = bx + a.

accessions in cluster 1 have distinct biochemical traits, potentially contributing to their enhanced pest resistance.

Discussion

The findings in this study demonstrate significant differences between wild tomato accessions and tomato cultivars in their whitefly resistance traits, trichome morphology, and terpene profiles. Wild accessions of *S. habrochaites*, *S. galapagense,* and *S. chilense* exhibited significantly lower number of nymphs per cm^2 than cultivars of *S. lycopersicum*, indicating the presence of intrinsic resistance mechanisms within these wild species.

Whitefly population dynamics during the growing season were influenced by environmental factors, such as rainfall, temperature fluctuations (Supplemental Table 2), and the presence of alternative host crops nearby. Warm daily air temperatures between 20 and 30 °C, without extreme variation, favor whitefly reproduction and development, whereas periodic rainfall can physically dislodge whiteflies from hosts, disrupting their lifecycle (Inoue-Nagata et al. 2016; Jeremiah et al. 2015; Rutz et al. 2023; Zeshan et al. 2015). The proximity of cotton and squash crops, which are preferred hosts for whitefly oviposition (Cui et al. 2012; Singh and Aggarwal 2024), adjacent to the experimental field, may have further contributed to reduced infestation pressure during the experiment. Although previous study at the same site detected the first adult whiteflies ∼23 DAT (Rutz et al. 2024), in this study they appeared at 30 DAT. In that prior study, cultivated genotypes averaged five adults per leaf, whereas wild accessions averaged 11 adults per leaf. Egg counts were comparable between groups (∼3–4 eggs/cm^2), whereas nymph densities were higher in cultivars (5/cm^2) than in wild accessions (3/cm^2). In the current study, under relatively low pest pressure, wild accessions maintained very low nymph densities (0.3 nymphs/cm^2), whereas commercial cultivars averaged 5.6 nymphs/cm^2. Adult populations also remained low, with wild accessions averaging 1.4 adults per leaf and cultivars averaging 1.8 adults per leaf. Similarly, egg densities were low in both groups, averaging 0.7 eggs/cm^2 in wild accessions and 1.8 eggs/cm^2 in cultivars, with no significant differences detected between genotypes, likely due to limited adult colonization during the sampling period.

Despite low egg densities, significant differences in nymph densities suggest post-oviposition resistance mechanisms, likely through antibiosis (Diniz et al. 2022). Specifically, *S. habrochaites* PI209978 and PI127826 exhibited near-zero nymph densities, high glandular trichome densities, and elevated levels of sesquiterpenes such as α-zingiberene, 9-hydroxy-10,11-epoxy-zingiberene, and 9-hydroxy-zingiberene, all known to impair whitefly development (Antonious and Kochhar 2003; Antonious and Snyder 2006; Bleeker et al. 2011; Dawood and Snyder 2020; Zabel et al. 2021). Previous studies indicate that specific wild accessions of *S. habrochaites*, *S. galapagense*, and *S. chilense* negatively influence whitefly oviposition and nymph development (Almeida et al. 2023; Andrade et al. 2017; Koeda et al. 2025). In contrast, tomato cultivars, particularly Apple Yellow and Cherry Bomb, exhibited significantly higher nymph densities (Fig. 1A), consistent with prior findings showing that cultivated tomatoes generally have lower inherent resistance to whiteflies compared with wild accessions (Ghosh et al. 2023; Rutz et al. 2024; Smith et al. 2019). Because the nymphs are sessile, they are especially susceptible to targeted control measures; reducing their population helps disrupt the whitefly lifecycle and reduces future infestations (Abubakar et al. 2022; Sani et al. 2020).

In this study, trichomes were classified as glandular or nonglandular to enable consistent density comparisons across genotypes. The analysis revealed that wild accessions have higher densities of glandular trichomes and lower nonglandular trichomes compared with cultivated tomatoes (Fig. 1B). Several studies have shown that specific glandular trichome types are associated with whitefly resistance, providing defensive mechanisms for the plant (Firdaus et al. 2012; Maliepaard et al. 1995; McDowell et al. 2011; Momotaz et al. 2010). In particular, types IV and VI glandular trichomes in *S. habrochaites* and type VI in *S. galapagense* and *S. chilense,* are associated with terpene production and whitefly resistance (Firdaus et al. 2012; Maliepaard et al. 1995; McDowell et al. 2011; Momotaz et al. 2010). These glandular trichomes not only form a physical barrier but also secrete defensive compounds, including terpenes, flavonoids, and acylsugars, which reduce whitefly attraction and feeding (Bleeker et al. 2011; Han et al. 2022; Kaur and Kariyat 2023; Zabel et al. 2021). In contrast, tomato cultivars demonstrated higher densities of nonglandular trichomes (up to 73 trichomes/μm^2 in Apple Yellow) but lacked glandular trichomes. This pattern suggests that domestication may have favored nonglandular trichomes for their structural purposes, such as providing physical protection or contributing to the plant's overall form, while reducing the presence of glandular trichomes that are essential for chemical defense (Kaur and Kariyat 2023; Miller and Tanksley 1990; Sade et al. 2020).

GC-MS analysis further confirmed the presence of distinct terpene profiles in wild accessions. *S. habrochaites* PI209978 and PI127826 produced high concentrations of α-zingiberene and its derivatives (9-hydroxy-10,11-epoxy-zingiberene and 9-hydroxy-zingiberene), which have been previously linked to pest resistance (Gonzales-Vigil et al. 2012; Kortbeek et al. 2023; Pizzo et al. 2024; Rutz et al. 2024). These terpenes likely deter whiteflies by reducing their attraction to the host plant or negatively impacting their survival. High terpene concentrations on the leaf surface can inhibit whiteflies from feeding or ovipositing (Boncan et al. 2020; Deletre et al. 2016; Wu and Baldwin 2010), disrupting their host selection process and encouraging them to avoid terpene-coated leaves, ultimately reducing infestation levels. The volatile nature of these terpenes provides antixenosis, a resistance mechanism that interferes with whiteflies' behavior and may indirectly attract their natural predators (Ninkuu et al. 2021).

Multivariate analyses focused on the key resistance traits that showed significant genotype differences, namely nymph density, glandular and nonglandular trichome densities, and terpene concentrations. Nymph density was the sole whitefly population parameter included, as adult and egg densities did not differ significantly among genotypes (Table 1). Notably, high densities of glandular trichomes were positively correlated with specific sesquiterpenes and negatively correlated with whitefly nymph density, particularly in *S. habrochaites*

Table 3. Terpene content in wild tomato accessions (*Solanum habrochaites*: G29258, PI126449, PI127826, PI134418, and PI209978; *Solanum galapagense*: LA1401; *Solanum chilense*: LA1932) and tomato cultivars (*Solanum lycopersicum*: LA3475, Cherry Bomb, Apple Yellow, Patsy, and Mountain Man) extracted from intact tomato leaflet trichomes.

						Terpene content (μg·g^{-1})[i]											
Compound	RT (min)	Quantitative ions (*m/z*)	Qualitative ions (*m/z*)	Molecular formula	Classification	LA1401	LA3475	LA1932	G29258	PI209978	PI127826	PI126449	PI134418	Cherry Bomb	Apple Yellow	Patsy	Mountain Man
α-pinene	5.55	136	93	$C_{10}H_{16}$	Bicyclic monoterpene	3.40 ± 0.73	<LOQ	0.64 ± 0.96	N.D.	15.99 ± 24.29	N.D.	N.D.	N.D.	0.59 ± 0.89	<LOD	0.96 ± 0.75	0.81 ± 0.21
camphene	5.84	136	121	$C_{10}H_{16}$	Bicyclic monoterpene	N.D.[iii]	N.D.	N.D.	N.D.	0.65 ± 0.98	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
similar to p-cymene[ii]	6.27	134	119			<LOQ	<LOQ	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	<LOQ	<LOQ	2.05 ± 0.27	2.23 ± 0.57
β-pinene	6.40	136	93	$C_{10}H_{16}$	Bicyclic monoterpene	<LOQ	N.D.	<LOD	N.D.	4.08 ± 6.21	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
4-carene[ii]	6.87	136	93	$C_{10}H_{16}$	Bicyclic monoterpene	2.85 ± 0.36	11.18 ± 4.99	1.28 ± 0.12	0.29 ± 0.44	1.85 ± 1.54	N.D.	N.D.	0.31 ± 0.46	12.34 ± 7.79	2.17 ± 0.90	23.04 ± 10.59	14.69 ± 4.45
α-phellandrene[ii]	6.95	136	93	$C_{10}H_{16}$	Monocyclic monoterpene	<LOD	<LOQ	<LOD	N.D.	1.90 ± 0.06	0.53 ± 0.10	N.D.	<LOD	1.51 ± 2.48	<LOQ	3.46 ± 1.53	2.47 ± 0.70
3-carene	7.07	136	93	$C_{10}H_{16}$	Bicyclic monoterpene	N.D.	N.D.	N.D.	N.D.	<LOQ	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
α-terpinene	7.20	136	121	$C_{10}H_{16}$	Monocyclic monoterpene	<LOQ	<LOQ	N.D.	N.D.	<LOQ	<LOQ	N.D.	N.D.	<LOQ	<LOQ	0.86 ± 0.70	<LOQ
p-cymene	7.37	134	119	$C_{10}H_{16}$	Monocyclic monoterpene	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD	<LOD
d-limonene	7.44	136	68	$C_{10}H_{16}$	Monocyclic monoterpene	N.D.	N.D.	N.D.	N.D.	N.D.	<LOQ	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
β-phellandrene[ii]	7.46	136	93	$C_{10}H_{16}$	Monocyclic monoterpene	<LOQ	5.67 ± 2.63	<LOD	<LOD	1.21 ± 1.83	<LOQ	N.D.	<LOD	3.81 ± 3.45	0.87 ± 0.76	10.11 ± 4.59	7.08 ± 2.15
β-Ocimene	7.84	136	121	$C_{10}H_{16}$	Acyclic monoterpene	N.D.	N.D.	N.D.	N.D.	0.44 ± 0.67	N.D.	N.D.	N.D.	N.D.	N.D.	<LOQ	N.D.
γ-terpinene	8.08	136	93	$C_{10}H_{16}$	Monocyclic monoterpene	<LOD	<LOD	N.D.	N.D.	<LOQ	<LOD	N.D.	N.D.	N.D.	N.D.	<LOD	<LOD
terpinolene	8.70	136	93	$C_{10}H_{16}$	Monocyclic monoterpene	0.15 ± 0.42	<LOQ	N.D.	<LOQ	0.69 ± 0.91	<LOQ	N.D.	N.D.	N.D.	N.D.	<LOQ	<LOQ
linalool	8.91	93	121	$C_{10}H_{18}O$	Acyclic monoterpene	N.D.	N.D.	N.D.	N.D.	<LOD	N.D.	N.D.	<LOD	N.D.	N.D.	N.D.	N.D.
δ-elemene[ii]	13.76	204	161	$C_{15}H_{24}$	Monocyclic sesquiterpene	2.42 ± 0.62	0.75 ± 0.56	N.D.	N.D.	<LOQ	<LOQ	N.D.	N.D.	<LOQ	N.D.	0.68 ± 0.56	1.45 ± 0.24
γ-elemene[ii]	15.54	204	161	$C_{15}H_{24}$	Monocyclic sesquiterpene	<LOQ	<LOQ	N.D.	N.D.	0.90 ± 1.36	3.25 ± 1.41	N.D.	N.D.	N.D.	N.D.	<LOQ	<LOQ
β-caryophyllene	15.33	204	93	$C_{15}H_{24}$	Bicyclic sesquiterpene	3.42 ± 1.02	1.07 ± 0.80	0.97 ± 1.46	10.24 ± 5.99	5.25 ± 4.34	N.D.	23.51 ± 10.24	9.11 ± 1.99	<LOQ	<LOQ	0.96 ± 0.81	1.57 ± 0.53
humulene	15.95	204	93	$C_{15}H_{24}$	Monocyclic sesquiterpene	<LOQ	<LOQ	0.96 ± 1.44	3.70 ± 2.06	1.19 ± 0.92	<LOQ	7.81 ± 0.96	2.85 ± 0.42	<LOQ	<LOQ	<LOQ	<LOQ
α-zingiberene	16.62	204	119	$C_{15}H_{24}$	Monocyclic sesquiterpene	2.89 ± 0.27	N.D.	1.44 ± 2.16	2.96 ± 4.44	27.77 ± 16.64	27.07 ± 0.94	N.D.	N.D.	N.D.	N.D.	N.D.	1.27 ± 1.01
β-sesquiphellandrene[ii]	17.11	204	69	$C_{15}H_{24}$	Monocyclic sesquiterpene	N.D.	N.D.	N.D.	N.D.	1.20 ± 1.80	<LOQ	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
nerolidol	17.76	204	121	$C_{15}H_{26}O$	Acyclic sesquiterpene	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	12.07 ± 079	N.D.	N.D.	N.D.	N.D.	N.D.
caryophyllene oxide	18.21	121	79	$C_{15}H_{24}O$	Bicyclic sesquiterpene	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	2.86 ± 0.56	N.D.	N.D.	N.D.	N.D.
9-hydroxy-zingiberene[ii]	19.34	222	32	$C_{15}H_{24}O$	Monocyclic sesquiterpene	N.D.	N.D.	N.D.	N.D.	30.19 ± 32.40	24.06 ± 13.00	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
9-hydroxy-10,11-epoxy-zingiberene[ii]	20.31	236	119	$C_{15}H_{24}O_2$	Monocyclic sesquiterpene	N.D.	N.D.	N.D.	N.D.	28.93 ± 37.83	46.82 ± 19.72	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.

[i] Data are presented as the mean concentration ± the standard deviation, with sample leaf of n = 3 and sample injection n = 3.

[ii] Putative identification.

[iii] N.D. = not identified.

LOD = limit of detection; LOQ = limit of quantification; RT = retention time.

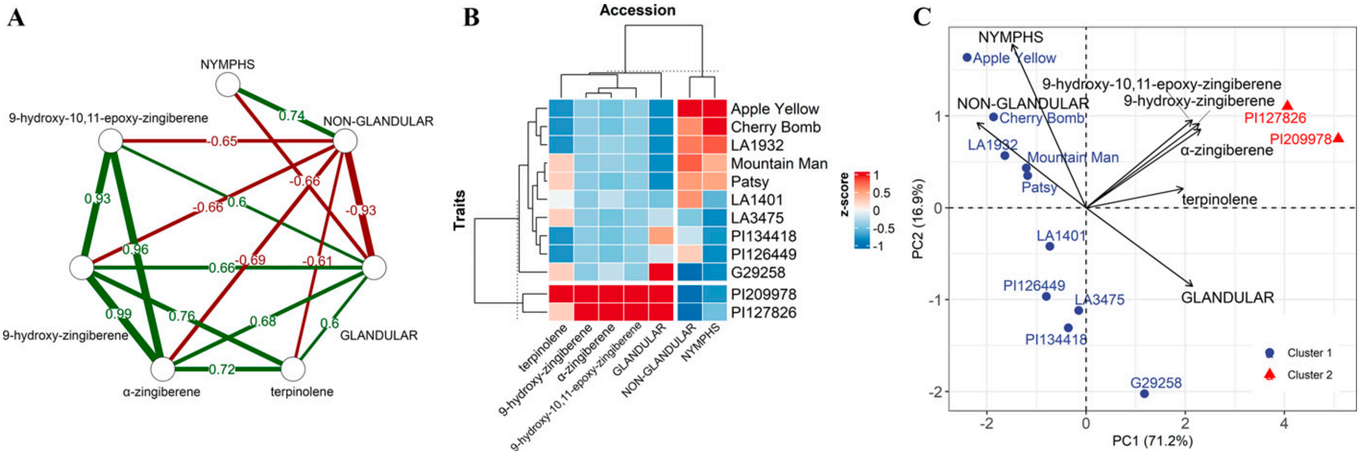

Fig. 2. Multivariate analysis of tomato accessions (*Solanum habrochaites*: G29258, PI126449, PI127826, PI134418, and PI209978; *Solanum galapagense*: LA1401; *Solanum chilense*: LA1932) and tomato cultivars (*Solanum lycopersicum*: LA3475, Cherry Bomb, Apple Yellow, Patsy, and Mountain Man) based on terpene profiles, trichome densities, and sweetpotato whitefly resistance. (**A**) The correlation-based network analysis (CNA) summarizes the significant correlations among trichome density, terpene abundance, and whitefly nymph density. (**B**) Cluster analysis reveals the relative expression of these traits, highlighting the biochemical and biological interactions. (**C**) The principal component analysis biplot identifies two distinct clusters, showing notable variations in terpene abundance and trichome types.

accessions PI209978 and PI127826. These accessions formed distinct clusters characterized by high levels of terpinolene, α-zingiberene, 9-hydroxy-zingiberene, and 9-hydroxy-10, 11-epoxy-zingiberene. This clustering pattern indicates a robust resistance phenotype differentiating these accessions from cultivars and other wild types. Although previous studies have highlighted the impact of glandular trichomes in reducing whitefly populations in *S. habrochaites* PI127826 (Almeida et al. 2023; Diniz et al. 2022; González-Arcos et al. 2018; Salazar-Mendoza et al. 2023), they did not report on terpene profiles or their correlations with trichome traits. Our previous studies identified *S. habrochaites* PI209978 (Pizzo et al. 2024) and PI127826 (Rutz et al. 2024) as having high α-zingiberene content, supporting the results presented in this study. The glandular trichomes on these accessions effectively store and release terpenes, which may contribute to repelling adults and maintaining low nymph densities.

Regarding data variability, the high standard error and *SD* values observed in some traits (e.g., egg counts, terpene levels) are typical in field trials involving insect populations, especially under low infestation. These high relative errors arise from low absolute values and natural biological variation, often including zero counts that inflate variance. Although data transformation techniques such as square root or log transformation are often used to stabilize variance, the original untransformed data were used in this study to maintain biological interpretability and transparency of the field observations. For terpene quantification, variation was driven primarily by biological differences among plants.

The strong resistance traits observed in wild accessions PI127826 and PI209978, especially their high glandular trichome density and production of specific sesquiterpenes, highlight the breeding potential of these accessions. Incorporating terpene-producing glandular trichome traits into commercial cultivars could reduce reliance on chemical insecticides, lower production costs, minimize environmental contamination, and preserve beneficial insect populations, aligning with IPM strategies (Abubakar et al. 2022; Divekar et al. 2022; Souto et al. 2021; Wang et al. 2020). Reducing pest pressure also may improve yield and fruit quality by limiting virus transmission and feeding damage (Douglas 2018), while minimizing pesticide residues for consumers, contributing to food safety and improved public health outcomes (Carvalho 2017).

Introgressing resistance traits from wild species remains challenging due to multigenic inheritance and linkage drag, where resistance genes are coinherited with unfavorable horticultural traits such as poor fruit set, small fruit size, or excessive vegetative growth (Chitwood-Brown et al. 2021; Rakha et al. 2017). Marker-assisted selection and advanced genomic tools will be essential to overcome these barriers (Sinha et al. 2023). In addition, wild accessions of *S. galapagense* and *S. chilense* warrant further exploration given the evidence of resistance observed in this study. The chemical diversity found in *S. habrochaites*, including terpenoids, acylsugars, fatty acids, and alkaloids, underscores the need for continued investigation using advanced analytical platforms such as liquid chromatography and ion mobility spectrometry (Kartowikromo et al. 2024; McDowell et al. 2011), to fully exploit wild tomato genetic resources for pest-resistant cultivar development.

Conclusion

This study demonstrated that wild tomato accessions, particularly *S. habrochaites* PI127826 and PI209978, exhibit significant resistance to whitefly nymphs compared with cultivars of *S. lycopersicum*. This resistance is primarily attributed to the high density of glandular trichomes and specific sesquiterpenes, such as terpinolene, α-zingiberene, and its derivatives, which may contribute to the observed resistance. The correlation between glandular-type trichome traits and terpene profiles with whitefly resistance reveals a strong association between increased glandular trichome abundance, elevated levels of specific sesquiterpenes, and reduced whitefly nymph density. These findings emphasize the potential of using wild tomato genetic resources in breeding programs to enhance pest resistance in tomato cultivars, offering an environmentally sustainable alternative to chemical whitefly control, contributing to IPM strategies in tomato production.

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